

THE ROSTRUM IN *PALORCHESTES* OWEN
(MARSUPIALIA: DIPROTODONTIDAE)
RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 3

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ABSTRACT

The rostral area of the skull is examined in all described species of the genus *Palorchestes* Owen and is shown to be characterized by massive dorsal excavation, associated with recorded and inferred reduction of the nasals and extreme elongation of the anterior of the palate. These features, taken in conjunction with the development of very large infraorbital foramina and the anteriorly directed facial area are interpreted as supporting a tapir-like proboscis in *P. painei* and probably in all known species of *Palorchestes*. The symphysis of the lower jaws is elongate in all forms and is narrow and deeply channelled dorsally, suggesting the presence of a long, flexible tongue which could have acted in conjunction with a proboscis in facilitating ingestion of herbage.

The genus *Palorchestes* is reasonably well-known in literature but has never been strongly represented in collections by specimens which show details of the cranial morphology. *Palorchestes* was defined by Owen (1874) as a macropodid and it was not until much later (Woods 1958) that its current systematic position within the Diprotodontidae was recognized. Three species have now been defined within the genus, these comprising the type species, *P. azael* Owen 1874, from Pleistocene sediments, *P. parvus* De Vis 1895, from the Chinehilla Sand of late Pliocene age and *P. painei* Woodburne 1967, from the Waite Formation of late Miocene or early Pliocene age.

Stirton *et al.* (1967) have attempted a phylogeny of the Diprotodontidae and have used Tate's (1948) subfamily, the Palorchestinae, for *Palorchestes* and for *Ngapakaldia* Stirton and *Pitikantia* Stirton from the Etadunna Formation of late Oligocene or early Miocene age. *Pitikantia* does not have crania preserved which present the rostral area. It is certain that *Ngapakaldia* did not have the type of cranial specialization observed in *Palorchestes*, and from what is currently known of *Pitikantia*, it is unlikely that dorsal excavation of the rostrum was a feature of that genus also.

The presence of an extensive modification to the rostral area of the skull in *Palorchestes* has been widely noted (Woods 1958; Woodburne 1967) but it was not until preparation of a near-complete cranium of *P. painei*, collected from the Waite Formation during the Ray E. Lemley expedition by the Queensland Museum in 1974, that the full extent of this structure and its possible significance became apparent. Less complete, but equally convincing material for both *P. azael* and *P. parvus* in the Queensland Museum collections also indicates the presence of comparable rostral structure in those species.

THE ROSTRUM IN *PALORCHESTES* PAINEI
WOODBURNE 1967

A reasonably complete description of the cranium of *P. painei* is provided in Woodburne (1967). The rostral area in QMF 9179 and QMF 9178 comprises more complete material on which the following supporting and supplementary comments are provided.

The rostral area is very elongated and relatively narrow and generally tapers anteriorly in lateral view. The incisor tooth row is projected more ventrally than the horizontal plane of the cheek teeth. Although slightly incomplete, the premaxillae are broader transversely than the anterior of

the maxillae giving the premaxillary alveolar margin a somewhat spatulate appearance. The palatal sutures between the premaxillae and maxillae are clearly defined, extending anterolaterally from the posterior border of the incisive foramina along their lateral borders then turning abruptly posterolaterally to the diastemal margins well posterior to the foramina, then continuing laterally, posterodorsally to near the narial notches. The premaxillae thus form broad wedges bordering the anterodorsal margins of the narial opening. Low, dorsomedial premaxillary spines are present, approximately above the level of I².

Ventrolateral diastemal margins are angular and the lateral surfaces posteriorly are gently concave above the margins. In occlusal view, the incisors present a broadly U-shaped outline. Dorsal margins of the thin posterior processes of the premaxillae are acute anteriorly, becoming sharply rounded and elevated to a higher angle to the horizontal. These margins are slightly rotated mesially. The anterior of the palate is moderately concave transversely with a medial sulcus extending anteriorly from the incisive foramina.

The maxillae form the bulk of the remainder of the rostrum. The palate is gently concave longitudinally posterior to the premaxillary-maxillary suture and is also concave transversely with an accentuated medial sulcus extending from the incisive foramina posteriorly to about the level of M². Laterally, the maxillae comprise long, deep bones wedging anteriorly to the angular diastemal margins. Towards the orbital margins, the lateral surfaces of the maxillae are sharply curved laterally, forming broad, near-vertical, transverse surfaces comprising an anteriorly directed facial region. These surround extremely large, elliptical, infraorbital foramina on each side, but that on the right side is much larger than on the left in QM F9179. However, in QM F9178 each foramen is relatively smaller. Lengths of the infraorbital canals are very short, opening posteriorly into variable, but large maxillary foramina.

The lacrymals extend moderately onto the facial region. Low frontal crests extend laterally as more pronounced 'brow' ridges, associated with the frontals, nasals and lacrymals, with the development of well-defined ventrolateral grooves anteriorly below the ridges. The nasals are very short, with nasal spines extending only slightly in advance of the narial notches.

The nasal cavity is deep anteriorly and very deep posteriorly, surrounded anteriorly by the premaxillae and posteriorly by the maxillae,

premaxillae and nasals. A bony nasal septum is present posteriorly. The floor of the cavity is occupied by fragments of bone, largely representing the remains of the vomer and parts of the septum. Anteriorly, the vomer is strongly and moderately deeply, inverted T-shaped in section.

THE ROSTRUM IN *PALORCHESTES PARVUS* DE VIS 1895

Woods (1958) has provided a basic description of the known cranial remains of *P. parvus* and the following comments, based on QM F789, amplify that study.

The rostrum is very elongate. It is relatively broader and tapers to a greater extent anteriorly in lateral view than in *P. painei*. The premaxillae are much broader transversely than in *P. painei* but are apparently not much broader than the anterior of the maxillae. The anterior alveolar border is flat and the incisors form a nearly rectilinear occlusal surface. Anterior to moderately high, medial, premaxillary spines, the dorsal surface is considerably extended and shelf-like, curving gently laterally to the alveolar margins.

Above the level of the incisive foramina and posterolateral to the premaxillary spines, the dorsal surfaces are deeply and variably excavated, leaving sharp, thin flanges of bone lining the nasal cavity anteriorly; lateral to these excavations, the bones are more robust, being broadly rounded dorsally at the anterior of the excavations and more acute posterolaterally. The palate is broadly concave transversely at the alveolar margin, but broad, ventral protruberences occur lateral to the incisive foramina in the area of the premaxillary-maxillary suture. Diastemal margins are flanged posterior to I³, becoming less so towards the maxillae. The premaxillary-maxillary sutures extend anterolaterally from near the posterior of the incisive foramina, then turning abruptly posterolaterally to the diastemal border and proceeding posterodorsally leaving thin wedges of bone extending as the dorsal rims of the narial opening. These wedges are considerably shallower anteriorly than in *P. painei*; the dorsal rims are somewhat directed mesially. Little of the anterior of the maxillae remains.

Although the infraorbital foramina are not preserved, part of one maxillary foramen is present, showing it to have been wide and presumably large. The infraorbital canals must have been short. The dorsal surface of the cranium is unknown, as is the anterior surface of the orbital area. No nasals are preserved, but the structure

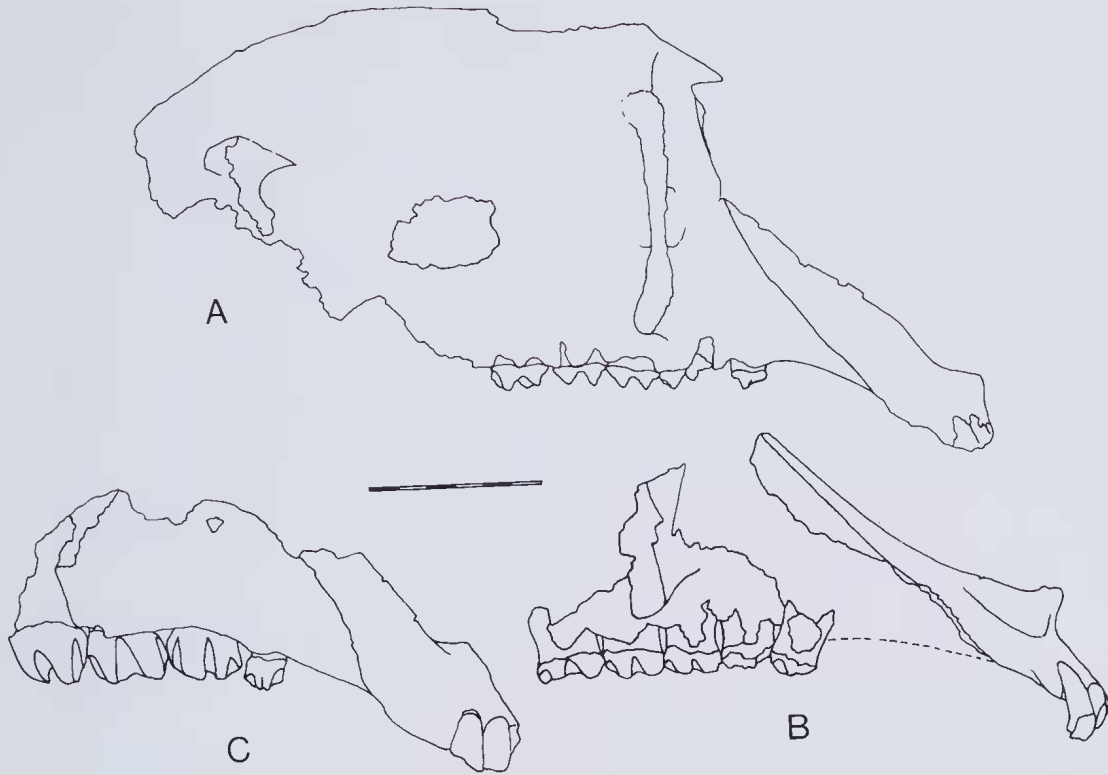


FIG. 1: Cranial remains in *Palorchestes*. A, *P. painei* (F9179), B, *P. parvus* (F789); C, *P. azael* (F3837), showing lateral extent of rostral modification. Scale in cms.

of the premaxillae suggests these must have been extensively retracted.

THE ROSTRUM IN *PALORCHESTES AZAEL* OWEN 1874

Owen (1874) describes the nature of the rostrum in *P. azael*. Existing descriptions are supplemented by the juvenile specimen, QM F3837.

The rostrum is elongate and relatively narrow, more like that in *P. painei* than in *P. parvus*.

The premaxillae are broad transversely, being much broader than the anterior breadth of the maxillae. The incisive alveolar border is broadly rounded and the upper incisors present a broad U-shaped occlusal outline. The medial premaxillary spines are relatively low and the dorsal surfaces anterior to these are broadly convex transversely to the alveolar margins. Posterior to I³, the diastemal margins are flanged for a short distance, then rounded from about the level of the premaxillary-maxillary sutures. The palate is anteriorly shallowly concave transversely, with a

deep, medial sulcus extending to the alveolar margin from the incisive foramina. The foramina are positioned well back and may be confluent. The premaxillary-maxillary sutures extend anterolaterally from near the posterior of the incisive foramina, then turn abruptly posterolaterally continuing posterodorsally from the diastemal margin. The posterior extensions of the dorsal parts of the premaxillae exist as broad wedges of bone capping the maxillae and bordering the narial opening, similar to those in *P. painei*. These are somewhat directed mesially. The palate has a relatively deep sulcus medially, posterior to the incisive foramina. Below the premaxillary processes, the maxillae anteriorly are laterally concave. Hollowing of the portion remaining of the facial area suggests that transverse, planar areas existed anterior to the orbits. No trace remains of the infraorbital foramina, canals or maxillary foramina. Although dorsal aspects of the skull are unknown, the nasals are interpreted as having been extensively retracted, based on the observed morphology of the premaxillae and the narial opening.

THE MANDIBULAR SYMPHYSIS IN *PALORCHESTES*
OWEN 1874

Woodburne (1967, figs. 23-4) has illustrated a specimen with a near complete symphyseal area in *P. painei*. The area is elongate, narrow, but deeply channelled, flaring anteriorly to accommodate large I_1 . The symphysis is also characterized by general down flexing of the anterior extremity of the dentaries which imparts a broadly longitudinally convex curvature to the dorsal symphyseal surface. Although this area in *P. parvus* is known only from a single specimen with no preserved teeth (QM F9180), no doubt exists regarding its identity. The structure is very similar to that in *P. painei*. In *P. azael*, a similar situation exists. The specimen QM F774, figured by Woods (1958, fig. 3), has a nearly complete symphyseal area. Although the ventral border is generally downflexed with regard to the bases of the rami, the anterior flexing present in both *P. painei* and *P. parvus* is lacking.

DISCUSSION

Although the dorsal surface of the eranium has not, as yet, been recovered in either *P. parvus* or *P. azael*, it is reasonable to assume from the known structure in *P. painei* and the morphology that is represented in the later material, that the rostral area of the skull in all three species was essentially similar. Detailed differences have been noted above, but none of these is considered to have had any marked effect on the general rostral structure or its overall functional significance.

The massive dorsal excavation of the rostrum is compatible with the presence in life of either an extensive rhinarium with anterodorsally directed nostrils or a proboscis, possibly similar to that in the eutherian tapiroids. Of these interpretations, the latter is considered most likely for the following reasons. The vomer apparently carried a cartilagenous septum well anteriorly, consistent with terminal nostrils directed anteriorly; the facial area of the skull is very flattened close to the rostrum and directed almost perpendicularly and at right angles to the axis of the skull; a prominent groove is present below the 'brow' ridge and this, together with the preceding point are both features presumably associated with the implantation of strong muscles; the variable, but large size of the infraorbital foramina, infraorbital canals and maxillary foramina are associated with the passage of an expanded infraorbital artery, vein and nerve, sufficient to supply a structure much larger and more functional than a rhinarium.

The degree of convergence with eutherian animals like tapiroids and litopterns is only superficial and *Palorchestes* has achieved its specialized cranial structure largely through modification of the premaxillae, rather than through maxillary modification. The deep, curved sulcus around the nasal notch in *Tapirus* has been only partly achieved in *Palorchestes*, while the rounded smooth anterodorsal aspect of the premaxillae has not been duplicated at all. Nasals in *Palorchestes* are retracted to a greater extent than in *Tapirus* suggesting that any proboscis in *Palorchestes* was not as well supported.

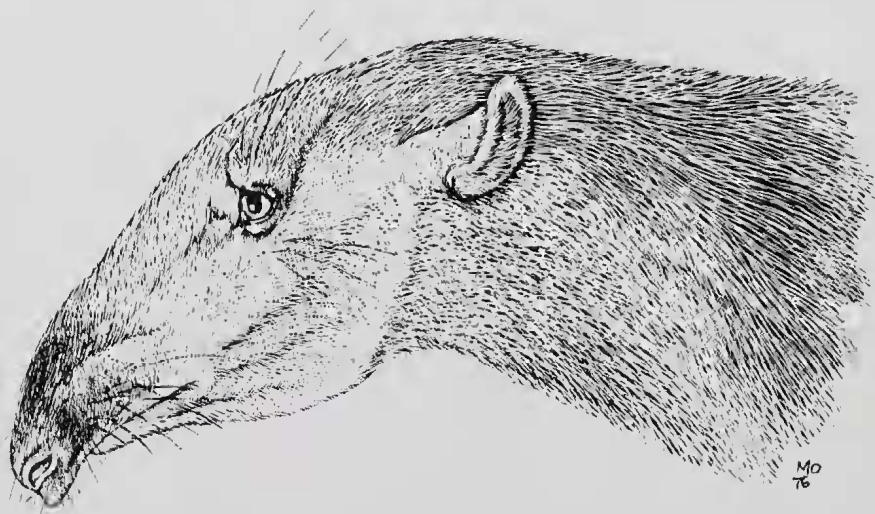


FIG. 2: Reconstruction of head of *Palorchestes*, based mainly on *P. painei*.

Retraction of the nasals in marsupials has also been reported by Bartholomai (1973) in the macropodids *Protemnodon roechus* Owen and possibly also *P. brehus* (Owen). These animals, however, are presumed to have possessed large rhinaria rather than functional proboscises.

The morphology of the mandibular symphysis in *Palorchestes* suggests that the tongue must have been long, narrow and flexible. Associated with the long diastema and the possible presence of a proboscis, these features would have been of benefit to *Palorchestes* in the gathering and ingestion of herbage before cropping by the broad series of upper and lower incisors.

The apparent consistency of these features and the peculiarity of the rostral morphology in particular, in *Palorchestes* suggest that the ancestry of *Palorchestes* was probably not associated with either *Ngapakaldia* or *Pitikantia* from the late Oligocene or early Miocene Etadunna Formation (Stirton 1967). Presumably these forms are closer to the generalized structural ancestors from which all three genera had evolved independently.

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